arrangement favorable to the particular curve or form of the stem imposed by the neuromuscular response. The work thus briefly reported upon was carried out last summer at the Scripps Institution for Biological Research, to the staff of which the writer is indebted for many courtesies.

[1] Contributions from the Zoological Laboratory of the Museum of Comparative Zoology at Harvard College, No. 287.

THE LIPS AND THE NASAL APERTURES IN THE GNATHOSTOME FISHES, AND THEIR HOMOLOGUES IN THE HIGHER VERTEBRATES

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Two distinctly different types of upper and lower lips, and a third type of upper lip are found in the gnathostome fishes, and they may be called the primary, secondary and tertiary lips.

The primary lips lie immediately external to the dental arcades developed in relation to the palatoquadrates and mandibulae, and they must, because of this position, have primarily lain but slightly, if at all, anterior to the oral plate of embryos. The primary cavity of the mouth lies internal to these lips. The hypophysial invaginations probably lay external to them, as they actually do lie external to the upper and primary lip of Petromyzon, and to both the primary and secondary upper lips of Amia and Acipenser.

The secondary lips of either side lie external to the primary ones, and have been developed from what was primarily simply a fold of the external dermis that lay posterior to the angle of the gape of the primary lips. The pressure of the musculus adductor mandibulae, where it passed around the angle of the primary gape, caused this fold to bulge forward across that angle, and its anterior surface was then presented antero-mesially. The crest of this fold then formed a secondary angle of the gape, which lay antero-lateral to the primary angle, and short secondary lips ran forward from it, in either jaw, to join the primary lips. These primarily short secondary lips then gradually extended forward in either jaw and ultimately there reached the median line and coalesced with their fellows of the opposite side, a band of the external surface of the head, lying between these secondary lips and the primary ones, thus being enclosed in the cavity of the mouth as a secondary

addition to it. Successive stages in this process are actually found persisting in the adults of living Plagiostomi.

The fold of the secondary upper lip of either side, running forward, passes either (1) between the primary upper edge of the mouth and the oral one of the two nasal apertures of its side, (2) across that aperture, (3) or between it and the aboral aperture, this depending upon the position of the nasal apertures relative to the upper edge of the mouth, upon the height of the fold of the secondary upper lip, and upon the length of the secondary gape of the mouth.

In all of the Teleostomi that I have been able to examine, the fold of the secondary upper lip passes oral to both the nasal apertures, as it also does in all of the Plagiostomi that I have been able to examine in which there is no naso-buccal groove, excepting only Heterodontus. Where there is a naso-buccal groove, the fold either (1) abuts against that groove and there abruptly ends (Scyllium canicula), (2) forms the lateral edge of that groove (Raia clavata), (3) or, as shown in Müller and Henle's[1] figures of Ginglymostoma concolor and Stegostoma fasciatum, passes between the nasal apertures and is continued mesial to them as a slight fronto-nasal ridge. The naso-buccal groove is simply the oral edge of the oral nasal aperture combined with the nasal-flap furrow, and results from the obstruction, by that aperture and the nasal flap, of the normal progression of the fold of the secondary upper lip. In Heterodontus francisci, where this groove is not found, the fold of the secondary upper lip passes between the two nasal apertures and is continued mesial to them as a well developed fronto-nasal flap, or process, and the posterior nasal aperture, lying oral to the fold of this lip, is enclosed in the secondary cavity of the mouth; but it still lies external to the primary cavity, exactly as the corresponding aperture does in all of the other Plagiostomi examined. In the Holocephali the conditions are too complicated to be here explained, but they have been derived directly from those in those of the Plagiostomi in which there is a naso-buccal groove. In the Dipneusti the fold of the secondary upper lip passes either between the two apertures or oral to both of them, the conditions in the one specimen of these fishes that I have been able to examine (Ceratodus) not giving definite indications as to this.

The so-called fronto-nasal process of those Plagiostomi in which there is a naso-buccal groove and in which the oral edge of the nasal flap is extended orally so as to bound the upper edge of the mouth, as in Scyllium canicula, is not the homologue of the fronto-nasal process of Heterodontus, for the nasal flap arises wholly independently of the

fold of the secondary upper lip and is not even crossed by that fold. This edge of the nasal flap thus does not form part of the secondary upper lip of the fish.

Cartilages are usually found developed in relation to the secondary lips of the Plagiostomi and Holocephali, and bones, with or without teeth, in the Teleostomi, the bones in the upper lips of the latter fishes forming a premaxillo-maxillary dental arcade which lies external to, and concentric with, the primary palatoquadrate, or so-called vomero-palato-pterygoid arcade.

In the Teleostomi, Holocephali and Dipneusti a dermal fold may be found lying aboral to the secondary upper lip.

In the Teleostei and Holostei this fold lies along and encloses the ventral edge of the lachrymal bone alone, or the ventral edges of that bone and one or more of the suborbital bones, and some part of the dorsal edge of the maxillary bone passes upward internal to the fold. The fold may accordingly be called the supramaxillary fold, for although it is, in these fishes, definitely related to the lachrymal bone, it is not so related to that bone in the Holocephali and Dipneusti. The fold, in the Teleostei and Holostei, is not continued forward in relation to the antorbital and dermal ethmoid bones, those bones being developed in relation to the antorbital section of the buccalis latero-sensory canal, the fold apparently being restricted to the suborbital section of that canal. In the Anacanthini, because of the marked anterior extension of the lachrymal bone, the fold is carried forward between the nasal apertures and the upper edge of the mouth, and is there continuous, in the median line, with its fellow of the opposite side; this apparently being a specific character of these fishes.

In the Holocephali and Dipneusti the supramaxillary fold passes aboral to the nasal apertures, and in these fishes the buccalis latero-sensory line passes aboral instead of oral to those apertures, and neither lachrymal, antorbital nor dermal ethmoid bones are developed in relation to it. In Chimaera the fold encloses the outer ends of a series of ampullary tubules, the external openings of these tubules lying near the edge of the fold and representing the places of origin of the related ampullary organs (Allis,[2]); and the coalesced folds of opposite sides form a semicircular line which circumscribes the nasal apertures, the upper lips, and the related naso-labial folds. In Ceratodus this fold has this same relation to the nasal apertures and the secondary upper lips, but it has here become a tertiary upper lip, and that band of the external surface of the head that lies between it and the secondary upper lip has been added to the secondary cavity of the mouth. The two

nasal apertures of Ceratodus are accordingly enclosed in the buccal cavity so enlarged, but as I can not trace the secondary upper lip in my specimen of this fish I can not tell whether they both lie in the tertiary addition to that cavity or one of them in that part of the cavity and the other in the secondary addition to it. No tertiary lower lip is formed, the tertiary upper lip simply overlapping the secondary lower lip. The anterior dental plates of this fish lie immediately internal to a lip that would seem to be a primary one, but as I cannot trace the secondary lips I cannot definitely affirm this. In Chimaera the corresponding plates lie internal to the primary lips, and hence belong to the palatoquadrate arcade.

In the Amniota the definitive upper lip is a secondary one, and it passes between the two definitive nasal apertures. Maxillary and premaxillary bones are developed in relation to it, and it is certain, from conditions found in certain of the Sauropsida, that the internal nasal aperture lay primarily between this arcade and the vomero-palatoquadrate arcade. The palatine bone of certain of these latter vertebrates, however, develops laterally and anteriorly, either approaching, coming into contact with, or even fusing with the maxillary or premaxillary bones, and in Chelone a ventral process of the bone turns antero-mesially and fuses with a ventral plate of the vomer anterior to the definite posterior nasal aperture. The posterior nasal passage of this animal thus lies between dorsal and ventral plates of both the vomer and the palatine, and the definitive choana, which is a secondary one, lies posterior to the ventral plates, the primary choana lying, as it normally should, anterior to the dorsal plates and hence to the bodies of the palatine and vomer. An accentuation of these conditions would withdraw the palatine bone entirely from its own arcade and leave it definitely anterior to the choana, as it is in the human skull, but it there nevertheless still lies posterior to the primitive choana.

In embryos of all of the gnathostome vertebrates above considered, the primary lips are represented in the edges of the primary stomodaeum, and hence not only in the deeper portions of the so-called maxillary and mandibular processes but also in the tissues that lie between the anterior (symphysial) ends of those processes. In embryos of the Teleostomi and Plagiostomi, excepting Heterodontus and those other Plagiostomi in which similar conditions may exist, the secondary lips are represented in the superficial portions of these same processes, and the maxillary processes, like the secondary upper lips of the adult, in growing forward pass oral to the nasal apertures, and they alone, or they together with an intervening portion of the primary upper lip, form the

definitive upper lip of the fish. In embryos of the Amniota, and unquestionably also in embryos of Heterodontus and those other Plagiostomi in which similar conditions may exist, the fold of the secondary upper lip is represented in the maxillary and fronto-nasal processes, the fold of this lip having here been cut into two parts by its encounter with the nasal groove; and these two processes form the definitive upper lip. With the formation of these embryonic so-called processes the primary stomodaeum has been converted into a secondary one, and a portion of the external surface of the head is in process of being enclosed in the cavity of the mouth. In embryos of Ceratodus the supramaxillary fold is superadded to the maxillary process, and the stomodaeum becomes a tertiary one.

In embryos of the Amniota the maxillary and fronto-nasal processes, representing the two parts of the fold of the secondary upper lip, lie primarily oral, respectively, to the lateral and mesial nasal processes as those processes are defined by Peter,[3] the fold of the secondary upper lip thus passing across the oral edge of the nasal groove, as it does in the adult Chimaera, and not, as in the adult Heterodontus, in the line of the nasal processes and hence that of the future nasal bridge. The break between the two parts of the fold then forms the so-called naso-buccal groove, which is thus simply a partially closed portion of the future posterior nasal aperture and not a specially developed groove which cuts across the secondary lip and leads into the secondary cavity of the mouth. The two parts of the fold never, in the Amniota, completely fuse with each other above the nasal groove, being always separated from each other by an epithelial line or membrane which is later broken through, and when a nasal bridge has been formed by the fusion of the nasal processes, the fold traverses that bridge. This bridge is thus the strict homologue of the bridge in the Teleostomi; for it is highly improbable that any new material has been brought to it by a simple fold of the dermis, as it is also improbable that such a fold, simply because it passes across the bridge, can in any way change the morphological character of that bridge. That band of the external surface of the head that lies between the primary and secondary upper lips forms the primitive palate, and the nasal processes take part in its formation only as they are included, in part, in that surface. Where the nasal bridge lies wholly aboral to the secondary upper lip, as in the Teleostomi, it does not form a primitive palate and can in no way be compared with it.

Aboral to the maxillary process of embryos of the Mammalia there is another process, or more properly a fold, which diverges slightly from the maxillary process and extends as far forward as the lachrymal

groove. This fold is well shown in Keibel's[4] figures of embryos of the pig, and must represent the supramaxillary fold of the Teleostomi, the lachrymal groove representing a part of the supramaxillary furrow of those fishes. The supramaxillary fold is apparently not continued onward anterior to this point, as it is in Chimaera and Ceratodus, and the Schnauzenfalte of His's[5] descriptions of human embryos, notwithstanding that it strikingly resembles the median portion of the supramaxillary fold of Chimaera and Ceratodus, is probably not a part of that fold. The lips and nasal apertures of the Mammalia could, accordingly, not be derived from those in Ceratodus without marked reversions, but they could readily be derived from those in Amia or Polypterus by the simple shifting of the secondary upper lip from a position oral to the nasal apertures to one between those apertures.

In the Amphibia the formation of the nasal appertures, as described by authors, is markedly different from that above set forth, but this is certainly due simply to condensations and abbreviations of the normal developmental processes, for the posterior nasal apertures of the adults of these vertebrates lie, as they do in the Amniota, between the primary and secondary dental arcades, and the nasal apertures of either side are, in embryos of certain of these vertebrates, connected by an epithelial cord (Gymnophiona) or line (Urodela) derived from the external epidermis; this cord or line certainly indicating the line where nasal processes have fused with each other above the nasal groove to form a normal nasal bridge.

[1] Müller, J., und Henle, J., *Systematische beschreibung der Plagiostomen*, 1841, Berlin, xxii + 200 pp., 60 Taf.

[2] Allis, E. P., Jr., *Q. J. Microsc. Sci., London*, N. S. **45**, 1901, (87–236), pl. 10–12.

[3] Peter, K., *Handbuch vergl. exper. Entwickelungslehre d. Wirbeltiere* von O. Hertwig, Bd. 2, Teil 2, 1906, (1–82).

[4] Keibel, Fr., *Anat. Anz., Jena*, **8**, 1893, (473–487).

[5] His, W., *Arch. Anat. Physiol., Anat. Abth., Leipzig* Jahrg. 1892, (384–424).

NATURAL AND ISOGONAL FAMILIES OF CURVES ON A SURFACE

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1. If F is a function of the coördinates of a point and ds is the element of arc length in any space, the curves along which $\int Fds$ *is a minimum* are said to form a *natural family of curves*. Such families include many interesting special cases. Thus if W is the negative potential function and h is a given constant of energy in a conservative